FOREST CENTERS OF EASTERN AMERICA.

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AN examination into the distribution of the forest trees of eastern North America develops the fact that there are several natural vegetation centers. Adams (: 02) called attention to the

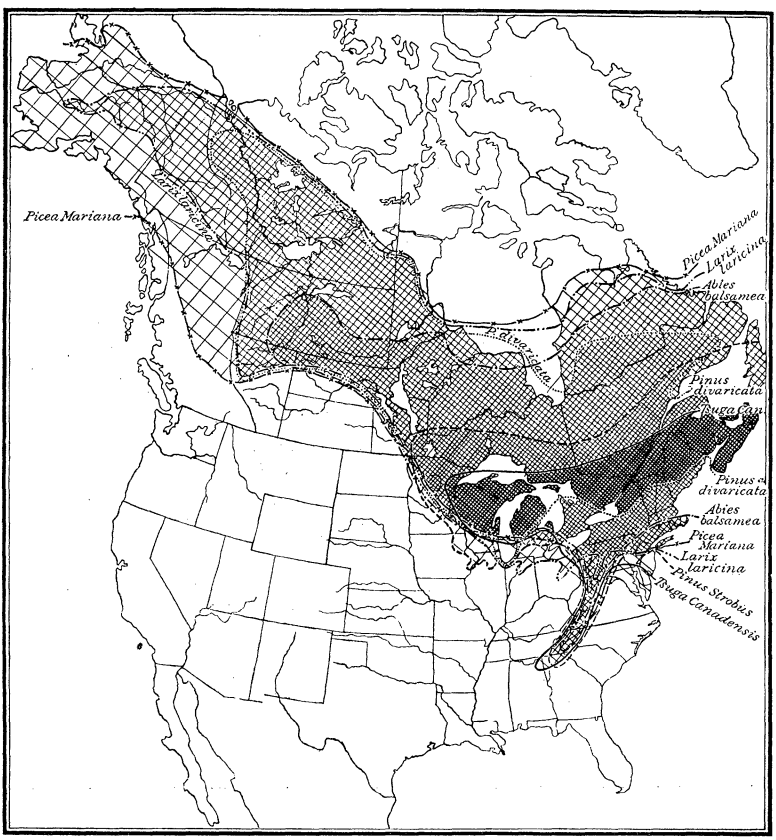

FIG. 1.— Map showing distribution of several of the dominant Conifers of the Northeastern Conifer center. The relative intensity of shading indicates the relative number of species found in the region.

distinctness of the biota of northeastern and of southeastern America, and showed that they are to be regarded as centers of

dispersal for the fauna and flora. In a former paper the writer (:03) pointed out that if the distribution of the characteristic bog plants be plotted on a map, the Laurentian region of Canada is indicated as their center of distribution. Within its limits, the plants have a wider range of habitats, attain a greater size, and are more abundant than elsewhere. It is also shown that

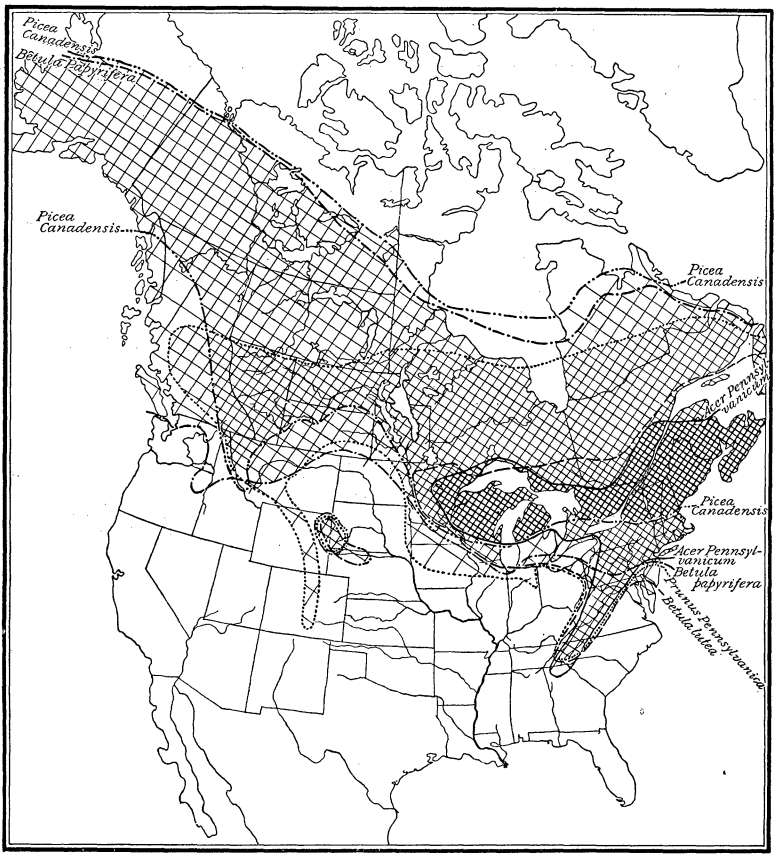

FIG. 2.—Map showing distribution of *Picea canadensis*, *Acer pennsylvanicum*, *Betula papyrifera*, *Prunus pennsylvanica*, and *Betula lutea* about the Northeastern Conifer forest center. The writer is under obligations to Professor Aven Nelson, Dr. P. A. Rydberg, and Mr. W. P. Holt for unpublished data which aided in the construction of this map.

the tree species are most limited in extent of dispersal, the bog shrubs have a wider range, while the herbaceous plants range from the Arctic seas to the Gulf of Mexico.

In using the term "center of distribution" it is not implied that the plants have necessarily spread from these centers, but that the complex of climatic factors most favorable to the development of this type of vegetation is here localized, and that as we depart from such centers we find conditions more and more unfavorable. This implies the elimination of such species as are most rigidly dependent upon definite conditions. Compare for example (Fig. 1) the distribution of *Pinus strobus* and *Tsuga canadensis* with that of *Picea mariana* or *Larix laricina* and note the intermediate dispersal of *Abies balsamea*. Fig. 2 shows the distribution of several other species and still further reinforces the suggestion that the St. Lawrence basin is a definite center about which is distributed a unique type of forest. It is floristically related to the forests of other parts of the continent but ecologically and climatically it is distinct.

The recognition and separation of these centers is of the greatest importance at the present time when there is so much activity along physiographic ecological lines. That there is a natural succession of plant societies in a given locality has long been recognized. Cowles (:01a) has shown that this succession may be correlated with the physiographic development of the region, because soil structure, water content, and slope are largely determined by it. Already the applicability of this hypothesis has been demonstrated in many parts of the United States.

But thus far little attention has been paid to the relation which the successive plant societies found in an area bear to their centers of distribution. In other words, the societies have been studied from their physiographic, but not from their geographic aspect. Such a geographic outlook, however, not only aids in the selection of the characteristic plants of the local habitat, but also throws light on the relative importance of the several societies. The geographic point of view is also necessary to furnish a suitable basis for comparing local meteorological data. Unless the climatic conditions of the centers of distribution of the societies are pointed out, the meaning of local climatic data is not apparent. Further, it is probable that in many areas the societies are not all members of the same geographic center,

so that comparisons with the conditions in two or more centers may be necessary to interpret fully the local data.

The geographic point of view is of the greatest importance in the study of regions intermediate between the great plant formations. In such localities there is a mingling of both species and societies which have spread from very different distribution centers. The local order of succession is usually a mixture of two or more orders, characteristic of as many centers. For example, in northern Michigan the successive societies (Whitford, :01) in the development of the forests, are: (1) xerophilous herbs, (2) the heath, (3) the coniferous forest, and (4) the maple-beech climax forest. While there can be little doubt but that this is the correct interpretation of the forest relationships in this region, there is a notable difference between these societies. The first three may be found anywhere in that region, while the last occurs only in areas favored by a rich soil, the climatic influence of the lakes, and the possibilities of migration from the southeastern deciduous forest. The first three societies are stages in the development of the climax forest of the Northeastern Conifer forest center, the last is the attenuated border of the climax stage of the southeastern Deciduous forest center. The first three stages are largely physiographic, while the last is also geographic, for it marks not only the succession of one society over another, but also the invasion and succession of one forest center over another.

In northern Pennsylvania and part of the mountains of New England, it appears from preliminary work that the successional relationship of the societies can only be traced by taking into account the fact that the societies of northern slopes and certain other edaphic situations are related to the Northeastern Conifer forest and form an order of succession *distinct* from that to which the societies of southern slopes and other favored situations belong.

Where best developed in the lower Ohio basin and Piedmont plateau, the climax stage of the Deciduous forest center (Fig. 3) is made up of many species of which the dominant are *Quercus alba, Magnolia acuminata, Acer saccharum, Fagus americana, Liriodendron tulipifera, Fraxinus americana, Quercus rubra*, and

Hicoria alba. Of these species the most hardy are the beech and the maple. In many places in the northern states the latter occupies areas almost to the exclusion of other trees, while within the southeastern center it is only one of many species in

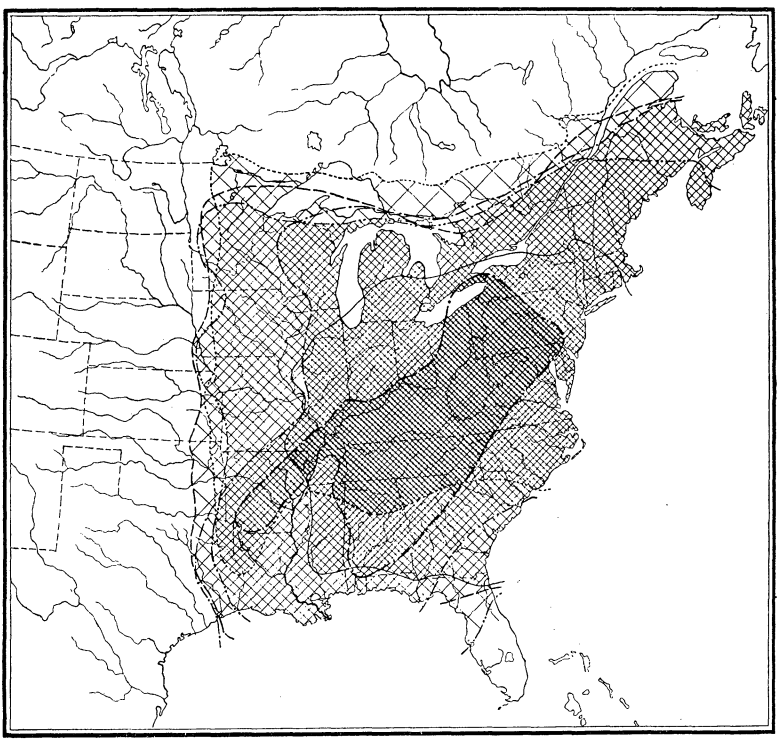

FIG. 3.— Map showing distribution of several trees belonging to the climax stage of the Deciduous forest center. – – – –, *Acer saccharum*; — — —, *Fraxinus americana*; — · — ·, *Fagus americana*; — – – –, *Quercus alba*; — — ·, *Magnolia acuminata*; ——, *Liriodendron tulipifera.*

the forest. This may be explained, not by the statement that the maple is a northern tree, but by the fact that its shade-enduring and shade-producing properties find no worthy competitor among the trees of the Northeastern Conifer formation, while at the south it is one of many species having the same characteristics.

In the mountain region of the southern Appalachians there is

an extension of the Northeastern Conifer forest. Probably it should be regarded as a subcenter, because of the large number of endemic forms present, and because many other species there attain their greatest development. There, it has been shown (Cowles, :01b) that the pine stage is followed by an oak society, which in turn gives way to the climax deciduous forest. This seems to correspond with the succession in certain parts of the

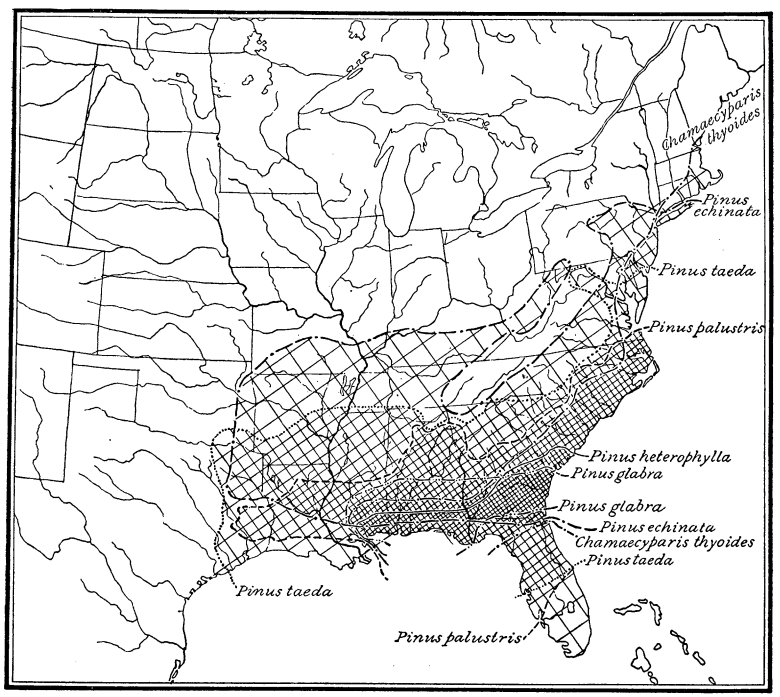

FIG. 4.— Map showing distribution of several trees belonging to the Southeastern Conifer forest center. *Chamæcyparis thyoides* is a common tree in the coastal swamps; the pines, with the exception of *Pinus glabra*, belong to the climax forest.

lower peninsula of Michigan, where the pines and the oaks both occur. Both localities are intermediate between the same two forest centers, and such a correlation is to be expected. The earlier stages in the succession are dominated by the Northeastern Conifers, while the last two are parts of the Deciduous forest center.

Furthermore in such intermediate regions, we may find two

distinct societies occupying the same or similar habitats. For example, in southern Michigan, the xerophilous bog societies and the hydrophilous swamp societies are so related. The former, however, are a part of the Northeastern Conifer forest, while the latter belong to the Deciduous forest succession. Consequently, where the bog societies are surrounded by oaks they

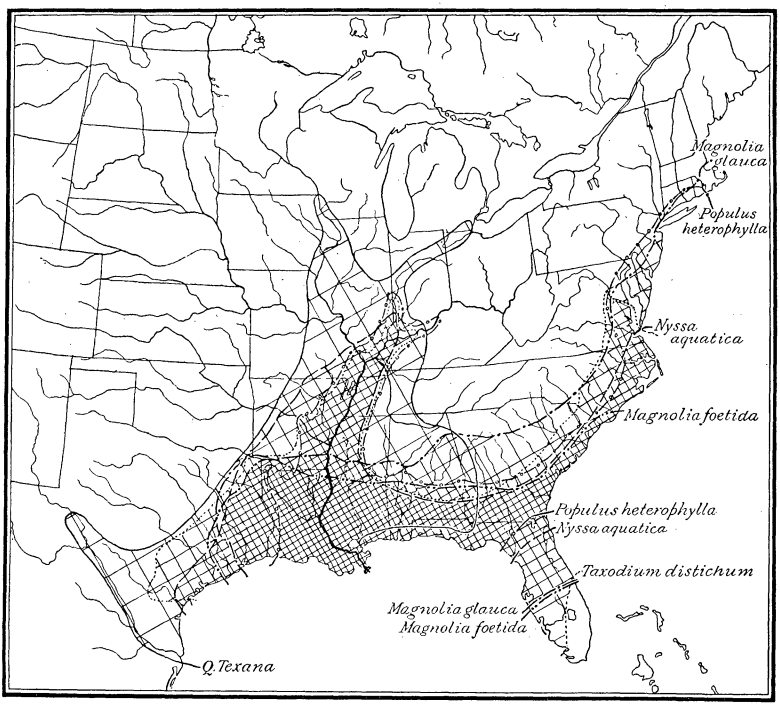

FIG. 5.— Map showing the distribution of some of the swamp trees of the Southeastern Conifer forest center. *Magnolia glauca, M. fœtida, Nyssa aquatica, Populus heterophylla, Taxodium distichum,* and *Quercus texana.*

bear no successional relationship, while the swamp societies change gradually into the oak and climax stages of the Deciduous forest. In such cases the geographic considerations are of equal importance with the physiographic, for the proper classification of the plant societies.

Turning to the coastal plain of the southeastern states, we find a dominant forest of Conifers, with mixed Conifer and broad-leafed societies on the low grounds. Here slight differ-

ences of elevation and relative geological age tend to be strongly expressed in the vegetation (Pinchot and Ashe, '97, pp. 143–181; Mohr, :01, pp. 107–133; Harshberger, :04, pp. 611–614). The Conifers probably represent the climax forest of this formation. The distribution of certain of its components is shown in Figs. 4 and 5. Several other associations of shrubs and trees might be similarly depicted and still further emphasize the identity of the Southeastern Conifer forest center. As shown by the accompanying maps and the descriptions of Smith, and Pinchot and Ashe, there is a mingling of societies of this center and of the Deciduous forest, in the region of the Piedmont plateau, which tends to obscure the recognition of the stages properly belonging to each.

On the southern half of the Florida peninsula is a fourth formation, made up largely of xerophilous tropical species. It really represents the northern border of a center which dominates the West Indies and tropical America. It may be designated the Insular Tropical forest center.

There appear then to be four centers of distribution in eastern North America: (1) the Northeastern Conifer, (2) the Deciduous, (3) the Southeastern Conifer, and (4) the Insular Tropical. Each is made up of many societies, which bear a definite successional relationship to one another.

With the exception of the tropical, each of these formations has its western border marked by gradation into the grasslands of the Great Plains. The local flora of any part of the intermediate prairie region is composed of societies from the plains and the adjoining forest centers. For example, take the succession of plant societies on the bluffs of the Kansas River in eastern Kansas. The pioneer society is made up of *Bouteloua hirsuta*, *Mentzelia oligosperma*, *Euphorbia marginata*, *E. dentata*, *E. petaloidea*, *Bœbera papposa*, *Artemisia ludoviciana*, *Aster sericeus*, *A. fendleri*, *Megapterium missouriense*, *Tragia ramosa*, *Baptisia bracteata*, *B. australis*, *Lacinaria punctata*, *Croton texensis*, *Solidago missouriensis*, and *Silphium laciniatum*. This society belongs to the flora of the Great Plains and has its eastern limit in the prairie belt. The shrub stage following this is made up principally of *Symphoricarpos symphoricarpos*, *Ceanothus ovatus*,

Rhus glabra, *R. aromatica*, *R. radicans*, *Cornus asperifolia*, *C. amomum*, and *Xanthoxylum americanum*. This society is of very different origin and represents the western border of the shrub stage of the Deciduous forest formation. The shrubs are succeeded by trees belonging to the same center, among which are *Juniperus virginiana*, *Ostrya virginica*, *Celtis occidentalis*, *Quercus acuminata*, *Cercis canadensis*, *Ulmus fulva*, etc. A very different combination of societies would be met with in similar situations in northwestern Minnesota or southeastern Texas because of the different centers involved.

The mapping of these centers naturally brings up the question of the climatic determinants of each. During glacial times the Northeastern Conifer must have been mixed with the Deciduous forest. Why are they so distinctly separated at the present time? What are the causes of the "prairie peninsula" in Iowa, Illinois, and Indiana; and the region of open forests adjoining it? Naturally we look for some method of mapping climatic data, which will show climatic centers in approximately the same positions as the centers of plant distribution. An examination of monthly, seasonal, and annual temperature and rainfall maps shows that neither of these factors alone can do this. Historical considerations may aid in explaining the relative positions of these centers, but are inadequate for the complete explanation of their present limits.

A method was accordingly sought by which temperature and moisture data could be combined in a single number. The fact that so large a part of all plant adaptations is directly or indirectly connected with transpiration, suggested that if the ratio of the rainfall to the evaporation were determined, a new basis for mapping would be at hand, which would involve several climatic factors. The depth of evaporation depends upon (T. Russell, '88) the temperature of the evaporating surface, the relative humidity of the air, and the velocity of the wind. These are the same climatic factors which most powerfully affect transpiration, and which must be of great importance in determining the geographic range of plants. Unfortunately, the only figures for evaporation available are those published by T. Russell for the year beginning July 1, 1887, and extending to July 1, 1888. They

represent the possibilities of evaporation from a free water surface inside the instrument shelters. Just as the figures for the rainfall do not represent the amount of water actually available for plants (since it includes the run-off, the part that evaporates, and that which sinks into the ground) so the figures for evaporation do not correspond to the water vapor actually given off by plants, because this is determined largely by the ecological adaptations of the individual plants. But the figures have a comparative value in both cases and when combined probably give a fairly correct idea of the distribution of these climatic factors in the eastern United States. The map was not extended to the western states owing to the paucity of data and the disturbing influence of the mountains. However, sufficient evidence is at hand to show that a desert center is clearly indicated in southern Arizona and California, and a forest center in the Puget Sound region. A comparison of the data for Colorado Springs and Pike's Peak indicates that the ratio increases from about 20 percent to 100 percent as one goes from the base to the summit of the Peak. This suggests the importance of taking other factors than temperature into account when explaining the distribution of the forests on mountains.

Turning now to the map (Fig. 6) showing the distribution of the rainfall-evaporation ratios in the eastern states, it will be noted that the Great Plains are marked by a rainfall equal to from 20 to 60 percent of the evaporation called for. The prairie region where forests are confined to the low grounds, is indicated by a ratio of from 60 to 80 percent. Its limits as indicated show a remarkable agreement with the actual distribution of the prairie. The region indicated by ratios between 80 and 100 percent is more or less coincident with the occurrence of "oak openings," "open forests," and "groves" on the uplands, and dense forests on the low grounds.

The southeastern area where the rainfall is from 100 to 110 percent of the evaporation, corresponds to the region of the Deciduous forest center. The distribution of the ratios above 110 percent in the region of the coastal plain is remarkably similar to the position of the Southeastern Conifer forest center.

In the southern Appalachians the ratio also rises above 110 percent and coincides with the occurrence of the southern extension of the northeastern forests. No data are available for the mountainous parts of Pennsylvania, so that this apparently isolated area may be climatically connected northward along the

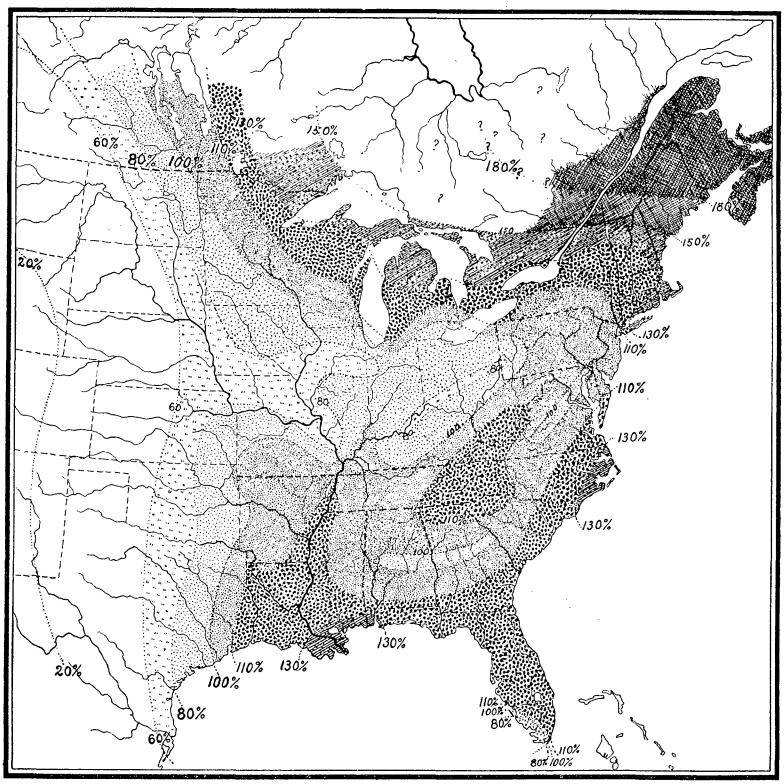

FIG. 6.— Map showing ratio of rainfall to evaporation expressed in percentages. (Compare with Sargent's map of the "Forests of North America," *10th Census Report.*)

higher mountain crests. The Northeastern Conifer forest center is marked by ratios above 100 percent and centering in the St. Lawrence basin. It is probable that the northern limits of this formation will not be indicated by the rainfall-evaporation ratios, for the factors commonly accepted (Schimper, :03, p. 168) as determining the northern limits of forests are very different from those causing the boundaries of other formations. It should

also be stated that since climates are constantly changing and effects may lag far behind their causes, no map of present climatic conditions can hope to do more than approximate the present distribution of plants. Geographic and historical relations must be constantly borne in mind.

SUMMARY.

It may be stated, by way of summary, that eastern North America is occupied by four great forest centers: (1) the Northeastern Conifer forest, centering in the St. Lawrence basin, (2) the Deciduous forest, centering in the lower Ohio basin and Piedmont plateau, (3) the Southeastern Conifer forest, centering in the south Atlantic and Gulf coastal plain, and (4) the Insular Tropical forest of the southern part of the Florida peninsula, centering in the West Indies. The term center as here used, implies the idea of distribution about a region where the plants attain their best development. Such vegetation divisions are not fixed, but move and increase or decrease in extent depending upon continental evolution and climatic change.

Each formation is made up of many societies, bearing a definite successional relationship to one another, which being dependent upon soil factors may be best correlated with physiographic changes. In regions intermediate between centers, the local order of succession is made up of societies from each of the adjoining formations.

It has been found that if the ratios produced by dividing the amount of rainfall by the depth of evaporation for the same station, be plotted on a map they exhibit climatic centers which correspond in general with the centers of plant distribution. Further, the distribution of grassland, prairie, open forest, and dense forest regions is clearly indicated.

This is explained by the fact that such ratios involve four climatic factors which are of the greatest importance to plant life, *viz.*, temperature, relative humidity, wind velocity, and rainfall.

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